

THE GENITALIA AND TERMINAL ABDOMINAL STRUCTURES OF MALE NEUROPTERA AND MECOPTERA WITH NOTES ON THE PSOCIDAE, DIPTERA AND TRICHOPTERA.¹

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Since the Neuroptera form one of the most important groups for a phylogenetic study of the higher insects, the discussion of the condition met with in them, and in the closely allied Mecoptera, is here offered as the basis of a later, more detailed consideration of the genitalia of the Trichoptera, Diptera, and other higher forms which can be more profitably taken up in separate articles, and are therefore only briefly referred to in the present paper. The homologies here proposed are based upon a more extensive consideration of the genitalia of the males of the lower insects, published in the June, 1918 issue of the Bulletin of the Brooklyn Entomological Society, and forms one of the series of phylogenetic studies there listed.

Many of the accompanying rough sketches were made from material kindly loaned by Mr. Nathan Banks, to whom I am likewise indebted for identifications of specimens, and for the loan of valuable literature dealing with the subject. Dr. R. J. Tillyard has also furnished me with a number of intensely interesting Neuroptera for study, in addition to much valuable literature on Australian Neuroptera and Mecoptera. Since I have been largely dependent upon the generosity of others for material in carrying on the present investigation, I would make use of this opportunity of acknowledging my deep obligation and expressing my very sincere gratitude to Mr. Banks and Dr. Tillyard for their ready and generous response to a request for aid in furnishing material and literature for such a study.

It is indeed surprising that so little has been published concerning the homologies of the genitalia of male Neuroptera and Mecoptera, which are of the utmost importance for the correct interpretation of the parts in the higher forms. Since those who have referred to the genitalia of the groups in question have, for the

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most part, contented themselves with merely describing the parts, without comparing them with other insects, the homologies here proposed must be regarded as purely provisional, until more intermediate stages can be obtained in order to determine what paths of development have been followed in arriving at the different types of genitalia here represented, or until suitable material can be obtained for dissections which cannot be carried out with dried, borrowed material, or from single specimens, upon which I have been largely dependent! On this account, it is to be hoped that those who have specialized in these groups, and therefore have access to a wider range of forms and more favorable material, will carry out a more extensive study of the genitalia, in order to arrive at a definite conclusion concerning many of the points which a lack of suitable material has made it impossible to determine.

It is quite generally conceded that the Sialid group should be rated among the most primitive representatives of the order Neuroptera.¹ I have therefore selected *Corydalis*, *Chauliodes* and *Neuronia* (which are the most instructive representatives of the group, available to me) as the basis for a comparison with the higher forms here discussed. In these insects (Figs. 4, 10, and 15), the digestive canal opens through an anal tubercle called the *tuberculum*, *anopilla*, or *proctiger* "ap." The two plates labeled "pa," one on either side of the tubercle "ap," were called *paraprocts* in a previous discussion of the parts in Neuroptera (Crampton, 1918), although I am not positive that they are the exact homologues of the paraprocts, or parapodial plates, of the Orthoptera and lower insects. In *Corydalis* (Fig. 15), the plate "pa" bears a pair of appendages "g," usually referred to as the *superior* and *inferior appendages of the gonopods*. For the sake of brevity they may be termed the *surgonopod* and *subgonopod*. The upper appendage, or surgonopod (Fig. 15) is the larger of the two, and appears to be the one to persist, when one of the two appendages is lost (as in Fig. 10, etc.).

Klapalek, 1903 (Bull. Int. Acad. Sci. Bohême), thinks that the gonopods of adult Trichoptera, etc. correspond to the "*Nachschiebern*" (anal prolegs?) of the larva. The gonopods of Neu-

¹ A study of the thoracic sclerites (which offer the most important characters for determining the relationships of insects) would indicate that the Neuroptera form a homogeneous group, which should not be further divided into "orders."

roptera, Mecoptera, etc., are usually homologized with the so-called "gonopods" of the Ephemera (Fig. 6, "s"), but, as was pointed out in a previous paper (Crampton, 1918), the structures labeled "s" in Fig. 6 of the Ephemera, are in reality *styli* which are segmented (*arthrostyloles*) in some forms, and are composed of a single segment in others. The segmented styli (*arthrostyloles*) labeled "s" in Fig. 6 of the Ephemera are borne on the plate "hy" situated *below* the male genitalia, and therefore cannot be homologous with the gonopods "g" of Figs. 10, 15, etc., which are situated *above* the male genitalia, and are not borne on the plate "hy," so that I have retained the term "gonopods" for the structures labeled "g," in Figs. 10, 15, etc., and have applied the designation "arthrostyloles" to the segmented styli of the Ephemera.

The so-called "*mammilliform processes of the penis*," labeled "pu" in Fig. 15, and described by Van der Weehle (Megaloptera, Coll. Baron de Selys Longchamps) in *Corydalis*, etc.; may possibly be homologous with the structure called the titillator by Brunner von Wattenwyl, 1876, in the Orthoptera, since the structures in question are situated above the opening of the ejaculatory ducts in *Corydalis*, etc. (as is the case in the Orthoptera). The structures labeled "pu" in Figs. 4, 10, etc., on the other hand, are possibly homologous with the so-called penis hooks, or "*penunci*" of lower forms. For the sake of convenience, however, all the structures labeled "pu" are here referred to as "penis hooks," regardless of their position with reference to the opening of the ejaculatory ducts.

Ventral to the penis hooks "pu" of *Chauliodes* (Fig. 10) is a cylindrical column-like structure "co" called the *columna* in a previous discussion of the parts in Neuroptera (Crampton, 1918). Below this is the so-called *genital valve* "hy," which is homologous with the *hypandrium* or *subgenital plate* of the lower insects. In the lower forms, the plate "hy" of the males frequently bears a pair of styli; but I have been unable to find these in any of the Neuroptera or Mecoptera thus far examined. The lobe-like structure situated above the plate "hy" and labeled "sl" in Fig. 15, may possibly be homologous with the so-called *sublobi* of lower insects (Crampton, 1918).

In the Psocid shown in Fig. 17, there is a *supraanal plate* or *epiproct* "sa" situated above the anal opening, on either side of which is a *parapodial plate* or *paraproct* "pa." I would interpret

the callosity labeled "c" in Fig. 17, as the remains of the cercus (which appears to be lost, or vestigial in most Neuroptera), and the spine-like process "g" as the homologue of the gonopod "g" of *Chauliodes* (Fig. 10), although I am not sure that these interpretations are correct, until other material has been examined to determine these points. The Psocidæ seem to be as closely related to the Neuroptera as any of the lower insects, and may be regarded as annectent between the Neuroptera and the Embiid Plecopteran group, from which have also branched off the Isoptera to which the Psocids are likewise closely related.

It is impossible to draw any definite conclusions concerning the relationships of the different Neuropteroid insects from a study of the genitalia alone; but the following points of similarity of structure in the different groups may be noted. In the Sialid group (Figs. 2, 4, 10, and 15), the hypandrium, or subgenital valve "hy" is comparatively small, and the gonopods "g" with the paraprocts "pa" are usually represented, although they are not always well developed. The anal tubercle or proctiger "ap" is present in most of this group, while the supraanal plate is usually wanting.

Ithone (Fig. 14) is considered as one of the most primitive representatives of the Neuroptera-Planipennia, and presents certain features suggestive of the condition found in the Sialid group. In the dried specimen of *Ithone* here figured (Fig. 14) there appeared to be a somewhat shriveled anal tubercle or proctiger "ap." The structures labeled "g" in Fig. 14, are not very like the gonopods "g" of the Sialid group (Figs. 10 and 15); but resemble somewhat more closely the structures labeled "g" in the Myrmeleonidæ (Fig. 7) which have been provisionally homologized with the gonopods. The penis hooks "pu" of *Ithone* (Fig. 14) are quite unlike those of the other forms here shown, and are covered by an arched roof-like structure. The hypandrium or subgenital plate "hy" is well developed in *Ithone*, unlike the condition occurring in the Sialid group.

Polystoechotes (Fig. 8), which is one of the Planipennia, has no well developed hypandrium "hy," and a structure labeled "co" in Fig. 8, may possibly represent the columna "co" of the Sialid group (Fig. 10). If this is correct, the terminalia, or terminal abdominal structures of some Planipennia are not unlike those of certain Sialids. In *Nemoptera* (Fig. 12), another of the group

Planipennia, the hypandrium "hy" is even larger than that of *Ithone* (Fig. 14, "hy"). In *Nemoptera* there is a large columna-like structure (Fig. 12, "co") which has been homologized with the columna "co" of *Chauliodes* (Fig. 10), and in addition, a small "epicolumna" labeled "p" has been developed. The columna "co" of Fig. 12 bears two lobes at its apex, suggesting a bipartite origin for this structure, and it is possible that it may represent the united penis hooks "pu" (Figs. 4, and 10) rather than the columna "co" of Fig. 10. I have provisionally homologized the lateral plates "pa" of Fig. 12, with the paraprocts "pa" of Figs. 17 and 15; but I am not certain that this is the correct interpretation of these structures. The structures labeled "g" in Fig. 12 may not be the true gonopods, but have been provisionally homologized with them.

Nymphes (Fig. 3) is regarded as one of the least modified forms related to the Myrmeleonidæ; but it has been very difficult to interpret the parts aright in this insect, and I am by no means certain that the conclusions here reached are the correct ones. The hypandrium "hy" is well developed in *Nymphes* (Fig. 3), and the structures apparently homologous with the penis hooks, labeled "pu" in Fig. 3, are very large and bear several "prongs." The structure designated "sa" in the figure probably represents the supraanal plate (epiproct), although it may possibly be homologous with the anal tubercle instead. I have provisionally homologized the lobes "cl?" of Fig. 3 with the copulatory lobes "cl" of the Mecopteron shown in Fig. 18; but there is a possibility that they should be homologized with the plates "pa" of Fig. 17 instead. The parts of *Nymphes* (Fig. 3) are disappointingly unlike those of the Ascalaphidæ (Fig. 1) and Myrmeleonidæ (Fig. 7), although the Ascalaphidæ are very similar to the Myrmeleonidæ in having a dorsal plate "sa" (Figs. 1 and 7), which has been interpreted as the suranal plate or epiproct, and two elongate lateral processes "g" provisionally homologized with the gonopods.

Mantispa (Fig. 5) resembles *Nemoptera* (Fig. 12) in having a well developed hypoproct "hy," within which is a slender structure labeled "co" (Fig. 5), which may possibly be homologous with the structure interpreted as the columna "co" in Fig. 12. The two plates "pa" of *Mantispa* (Fig. 5) are possibly homologous with the plates labeled "pa" in Fig. 12 of *Nemoptera*.

Raphidia (Fig. 16) does not seem to be very like any of the other Neuroptera here figured so far as its terminal structures are concerned. It has an arched dorsal plate "sa" which may represent the supraanal plate, or epiproct, beneath which are two processes "g," provisionally homologized with the gonopods "g" of Fig. 10, etc. The two penis hooks "pu" of *Raphidia* (Fig. 16) are apparently homologous with the structures labeled "pu" in Fig. 5 of *Mantispa*, and the median hook "mu" of Fig. 16, is possibly homologous with the median hook "mu" of Fig. 5, although I am somewhat at a loss to account for the homologies of the structure "mu" of Figs. 5 and 16, in other forms.

The Coniopterygidæ (Fig. 11) are too small and highly specialized for one to be able to make very much out of a study of their parts. The hypandrium "hy," of Fig. 11, is comparatively well developed, and the structures labeled "pu" appear to represent the penis hooks "pu" of the other Neuroptera. The terminal structures of the Coniopterygidæ appear to resemble those of the Planipennia, as much as any other Neuroptera.

Turning next to the consideration of the genitalia and terminalia of the Mecoptera, we find two types represented, namely, those with forceps-like gonopods (*e. g.*, Figs. 24, 20, 23, 27, and 28) which are of extreme length in *Merope* (Fig. 24 "g"), and a second type represented by the *Bittacus*-group (Figs. 18 and 22) in which the gonopods are not developed in the form of forceps-like structures. In Vol. 27, page 298 of the *Entomological News* for July, 1916, I suggested that the *Merope* type of Mecoptera represented a suborder called the "Promecoptera," in which the wings present a very primitive venation, the head is not greatly elongated, etc. *Merope*, however, is quite closely allied to the other members of the *Panorpa*-group, and should be included in it, so that there are but two principal groups of living Mecoptera (the *Bittacus*-type and the *Panorpa*-type) and these two might be considered as representing two suborders of the Mecoptera, although they are more probably of merely superfamily rank. Tillyard, 1917 (Proc. Linn. Soc. N. S. Wales, 42, p. 188), applies the term Promecoptera to a new order of fossil insects which in certain respects resemble the ancestors of living Mecoptera.

Although I feel certain that such forms exist, I have been unable to find any Neuroptera in which the gonopods are in the form of

jointed forceps-like structures as in the *Panorpa*-group (Figs. 24, 23, etc.), and since the *Bittacus*-group seems to be as primitive as any, so far as the terminal structures and genitalia are concerned, I have used them as the basis for a comparison with the other Mecoptera and the Neuroptera. *Bittacus* (Figs. 18 and 22) seems to resemble *Nymphes* (Fig. 3) as much as any Neuroptera, in respect to its terminal structures; and the median terminal appendage "sa" of Figs. 18 and 22, which is either homologous with the supraanal plate (epiproct) or with the anal tubercle (proctiger), is apparently the homologue of the median terminal structure labeled "sa" in Fig. 3 of *Nymphes*. The copulatory claspers "cl" of *Bittacus* (Figs. 18 and 22) are possibly represented by the lobes labeled "cl?" in Fig. 3 of *Nymphes*, and are analogous to, if not actually homologous with, the copulatory claspers, "cl," of the Phasmid shown in Fig. 9, and doubtless had a similar origin. The claspers "cl" are very large in *Bittacus strigosus* (Fig. 18); but are much smaller in *Bittacus pilicornis* (Fig. 22). Correlated with the greater development of the claspers "cl" of *Bittacus strigosus* (Fig. 18), there is a greater development of the appendages labeled "c" (which are provisionally homologized with the cerci) than in *Bittacus pilicornis* (Fig. 22), although in the latter insect, the median appendage "sa" is proportionately somewhat larger than that of *B. strigosus* (Fig. 18). In both insects shown in Figs. 18 and 22, there occurs a pair of closely approximated hooks labeled "pu," provisionally homologized with the penis hooks. Between them there projects a spiral thread or spirofilum "sf," wound like a watch spring. It is possible that this spiral thread represents the columna "co" of Fig. 10. At the base of the hooks "pu" (Figs. 18 and 22) is a pair of appendages labeled "g?" which may represent the gonopods of the other Mecoptera, although I would not insist upon this interpretation. Miyake, 1913, on the other hand, regards the hooks "pu" (Figs. 18 and 22) as parts of the "pedes genitales."

In comparing the *Panorpa*-group with the *Bittacus*-type, one of the most noticeable features is the lack of development of the claspers "cl" in the former group. On the other hand, the gonopods "g" are greatly developed in the *Panorpa*-group (Figs. 24, 20, 23, and 27). I am not sure that the distal segment of the gonopod "g" of Fig. 23 is homologous with the appendage labeled

"g?" in Fig. 18, since it may correspond to the structure labeled "pu," instead; but I have provisionally adopted the interpretation indicated by the labeling. In most of the *Panorpa*-group there are one or two pairs of dorsal valves (dorsovalvæ), "dv" of Figs. 21, 23, 24, etc., and a pair of ventral valvæ (ventrovalvæ), "vv" of Figs. 23, 26, etc., and it is possible that certain of these valvæ may represent the penis hooks of Neuroptera, etc.

The anal tubercle "ap" of Fig. 21, bears at its base a pair of appendages "c" whose location suggests that they are homologous with the so-called cerci "c" at the base of the median terminal structure "sa" of Figs. 18 and 22. On this account, I would consider the structure "ap" of Fig. 21 as homologous with the structure "sa?" of Figs. 18 and 22, although I am not certain whether the structure labeled "sa?" in Figs. 18 and 22 is the epi-proct "sa," or the proctiger "ap," of other insects. Tillyard describes a pair of segmented cerci in *Nannochorista* (Fig. 28, "c"), which appear to be homologous with the structures labeled "c" in Figs. 21, 23, etc., and on this account I have interpreted the latter structures as the cerci. I am not certain of the correctness of my interpretation of the structures labeled "c," as the cerci, and the structures labeled "dv," as the dorsal valvæ, in Fig. 24 of *Merope*; but have provisionally adopted this method of homologizing them. The projecting ventral process "co" of Fig. 26, may be homologous with the columna, and if the latter is represented by the coiled filament "sf" of Figs. 18 and 22, the structure labeled "co" in Fig. 26 is doubtless to be homologized with the coiled filament "sf" also.

The phallus "pe" is large and prominent in *Boreus* (Fig. 20), and the hypandrium "hy" is well developed in this insect. In *Panorpodes* (Fig. 27) the structure which is here interpreted as the hypandrium "hy" shows a marked tendency to become long drawn out and furcate, although the cleft at its apex is not very deep. In the Panorpid shown in Fig. 26, however, the hypandrium "hy" is deeply cleft, and the two arms of the fork are comparatively long and narrow. The character of the hypandrium fork, the valvæ, etc., should be as valuable features for the purpose of classification as any structures, and it is surprising that they are not more employed in taxonomic keys.

The gonopods "g" of the Mecoptera here figured are composed of two segments. The basal one "pa?" of Fig. 23 may possibly

correspond to the paraprocts "pa" of the Neuroptera (Fig. 15, "pa"), although the elongate basal segment "g" of the gonopod of the very primitive Mecopteron *Merope* (Fig. 24) is nothing like the paraprocts in character, and this casts some doubt upon the supposition that the basal segment of the gonopods of the Mecoptera in general corresponds to the paraproct.

As was mentioned above, it is very strange that no Neuroptera have been described in which the gonopods are of the type represented in *Merope* (Fig. 24, "g") which is a very primitive Mecopteron in many respects, since the tendency toward the development of forceps-like gonopods occurs in many Mecoptera, Diptera, Trichoptera and other forms descended from Neuropteroid-like forebears. The gonopods "g" of such Mecoptera as *Merope* (Fig. 24) are apparently the prototypes of those found in certain Diptera such as the Chironomid *Clunio* (Fig. 25, "g"). The occurrence of this type of gonopod in the Diptera lends further weight to the view that the Mecoptera are very like the ancestors of the Diptera.

Some Trichoptera have well developed gonopods, such as those of *Philopotamus* (Fig. 30, "g"), as might be expected from other evidence that the Trichoptera are rather closely related to the gonopod-bearing Mecoptera, both groups having apparently descended from Neuropteroid ancestors. The structures labeled "cl" occurring on either side of the supraanal plate "sa" of *Philopotamus* (Figs. 30 and 13) resemble cerci in some respects; but have been provisionally homologized with the clasper lobes "cl" of other forms. Klapalek, 1903, refers to similar appendages in the Trichoptera as the "appendices præanales."

As far as the relationships of the orders here discussed are concerned, I would maintain that the Neuroptera, Mecoptera, Diptera, Trichoptera and Lepidoptera constitute a superorder, the *Panneuroptera*, certain of whose members exhibit a tendency toward the formation of hairs or scales on the wings (*e. g.*, certain Myrmeleonids, a few Panorpid, the Psychodid Diptera, etc., in addition to many Trichoptera, and most Lepidoptera), and in most of which the meso-thoracic coxæ, at least, are divided into a veracoxa and merocoxa (see Crampton and Hasey, 1915, "The Basal Segments of the Leg in Insects;" *Zoöl. Jahrb., Abt. Anat.*, 39, p. 1-), the mesothoracic and meta-thoracic coxæ are usually

approximated, there is usually a sternal fulcrum of the coxa (Crampton and Hasey, l. c.), and other characters showing that they have much in common.

I would group the Psocidæ, Thysanoptera, Mallophaga, Anoplura (Pediculidæ), Hemiptera and Homoptera in another superorder, the *Panhomoptera*, but by so doing, I would not minimize the close relationship of the Psocids to the Neuroptera, and the close approach of the Hemipteroid lines of development to those of the Mecoptera and Diptera. The Hymenoptera are closely allied to both the Psocidæ and the Neuroptera, and I have been unable as yet to determine in which of the two superorders they should be placed.

In connection with the discussion of the interrelationships of the orders of insects, it may be of some interest to note that it would appear that in the interesting little Crustacean *Bathynella* we have a form very like the common ancestors of the Insecta and "Myriopoda" (*sensu lato*). *Bathynella* belongs to a very ancient group of Crustacea, and the number of segments composing its body, the character of its appendages (which are lacking on the last segments), etc., are all in accord with the view that it is very like the ancestors of the Proturan insects. *Bathynella* is also very like the probable ancestors of the Symphyla-Pauropoda, a group which has departed but little from the condition characteristic of the ancestors of the "Myriopoda" as a whole.

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The following articles treat only of the Neuroptera and Mecoptera. Bibliographies of works on Trichoptera, Diptera, etc., will be given in articles dealing with the genitalia of these groups.

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See also articles by Banks, Tillyard, and other systematic articles on Neuroptera and Mecoptera.

ABBREVIATIONS.

ap = Anal tubercle, anopapilla, or proctiger.	g = Gonopods, or their homologues.
c = Cerci, or vestiges of cerci.	hy = Subgenital valve, or hypandrium.
cl = Copulatory lobes, or copulobi.	mu = Median hook, or medianus.
co = Columna.	sa = Supraanal plate, or epi-proct.
dv = Dorsal valvæ, or dorso-valvæ.	sf = Spiral filament, or spirofilum.
pa = Parapodial plates, or paraprocts.	sl = Sublaminæ.
pe = Phallus.	t = Terminal filament, or telofilum.
pr = Preepiproct.	vv = Ventral valvæ, or ventro-valvæ.
pu = Penis hooks, or penunci.	
s = Jointed styli, or arthrostyles.	
ep = Epicolumna.	
f = Pendent filaments.	

EXPLANATION OF FIGURES.

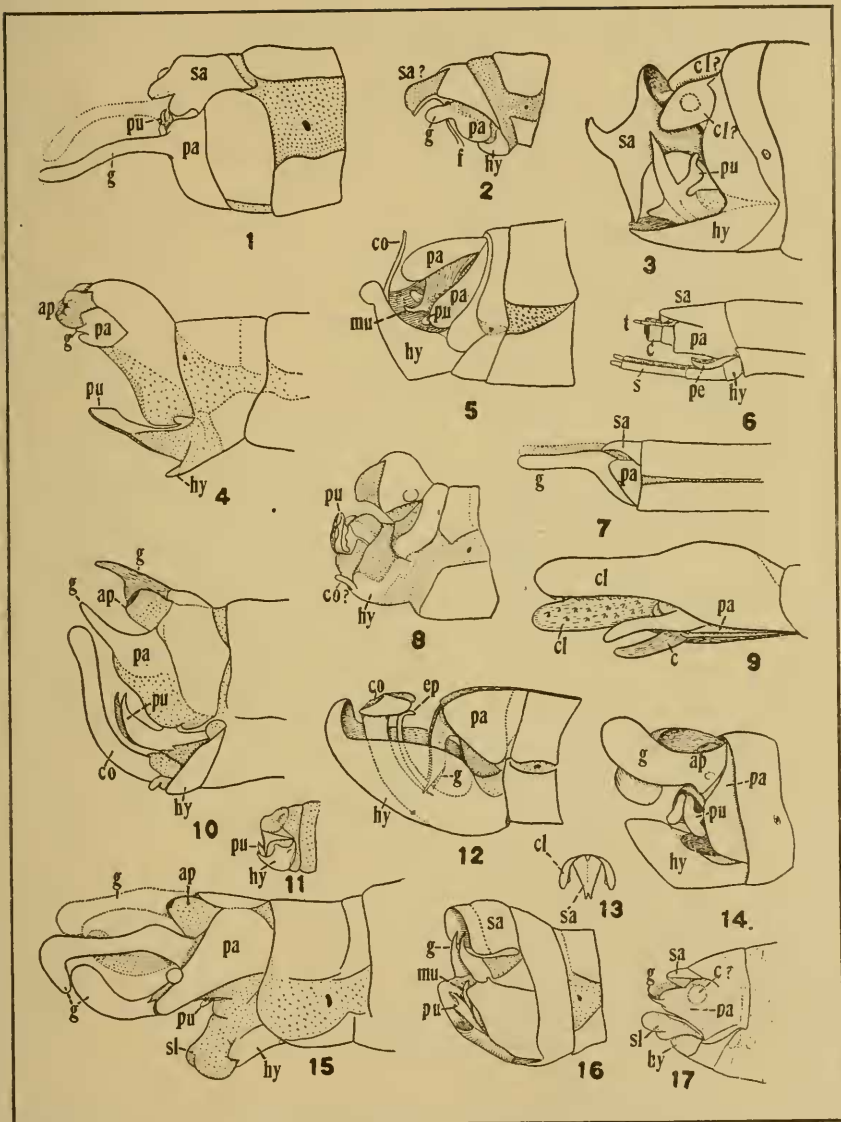
Unless otherwise stated, figures are of terminal structures and genitalia.

Plate II.

- Fig. 1. Lateral view of an Ascalaphid (Neuroptera).
 Fig. 2. Lateral view of *Sialis* (Neuroptera).
 Fig. 3. Lateral view of *Nymphes myrmeleonides* (Neuroptera).
 Fig. 4. *Nigronia serricornis*, Say (Neuroptera), lateral view.
 Fig. 5. *Mantispa brunnea*, Say (Neuroptera), lateral view.
 Fig. 6. *Ephemera varians?* (Ephemeroidea), lateral.
 Fig. 7. *Brachynemurus longicaudus*, Br. (Neuroptera), lateral view.
 Fig. 8. *Polystachotes punctatus* Say (Neuroptera), lateral view.
 Fig. 9. *Clitumnus lorigatus*, Br. (Mantidæ), lateral.
 Fig. 10. *Chauliodes pecticornis*, L. (Neuroptera), lateral.
 Fig. 11. A Coniopterygid (Neuropteran), lateral.
 Fig. 12. *Nemoptera sinuata* (Neuroptera), lateral. Restored from crushed specimen.
 Fig. 13. *Philopotamus* sp. n. (?) (Trichoptera), dorsal view of lobes and suranal plate.
 Fig. 14. *Ithone*, sp. (probably *I. fusca*), Neuropteran, lateral view.
 Fig. 15. *Corydalus cornutus*, L. (Neuroptera), lateral.
 Fig. 16. *Raphidia oculata*, Banks (Neuroptera) lateral.
 Fig. 17. Lateral view of a Psocid, probably *Psocus venosus* Burm. It is a large winged form found in colonies on pines near Amherst, Mass.

Plate III.

- Fig. 18. *Bittacus strigosus*, Hag. (Mecoptera), lateral.
 Fig. 19. *Panorpodes* (Mecoptera) from N. Carolina, dorsal view of apex of genital segments.
 Fig. 20. *Boreus brumalis*, Fitch (Mecoptera), lateral.
 Fig. 21. *Panorpa lugubris*, Swed. (Mecoptera) dorsal view of genital segments, the upper plate "pr" of Fig. 23 removed, and anal tubercle bent back.
 Fig. 22. *Bittacus pilicornis*, Westw. (Mecoptera), lateral.
 Fig. 23. *Panorpa lugubris*, Swed. (Mecoptera) lateral.
 Fig. 24. *Meropa tuber*, Newm. (Mecoptera) dorsal.
 Fig. 25. *Clunio bicolor*, Kieffer (Diptera), based on Fig. 1, Plate 4, of fascicle 42 on Chironomid Diptera, by Kieffer, 1906 (Genera Insectorum).



CRAMPTON—Genitalia and Terminal Abdominal Structures.